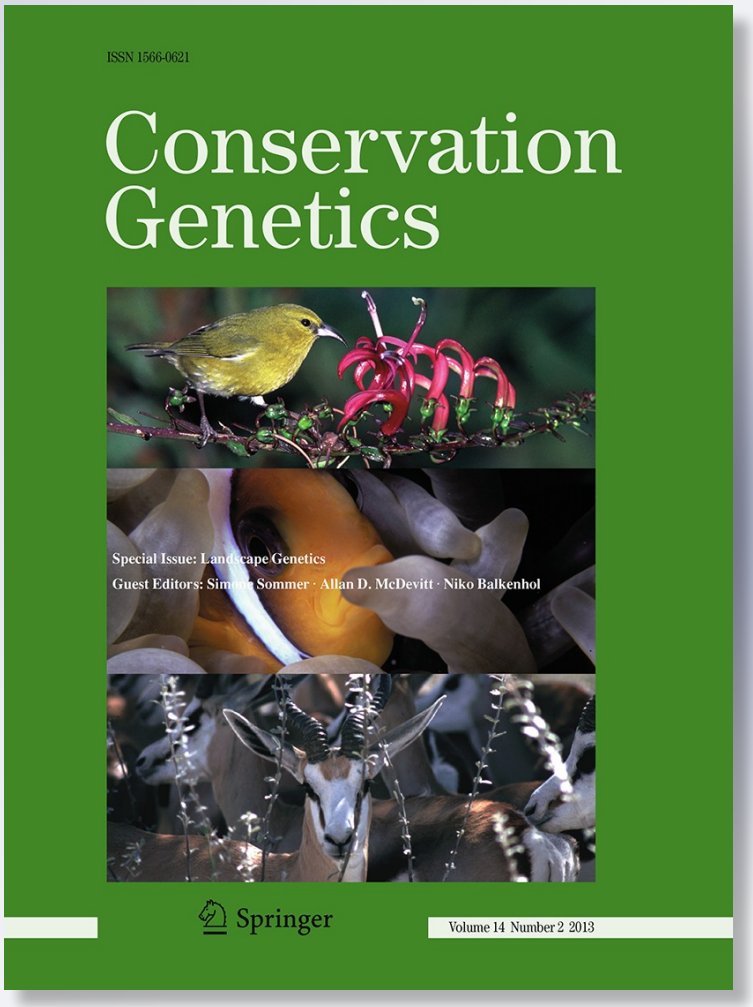
Individual variation in dispersal associated with phenotype influences fine-scale genetic structure in weasels

Allan D. McDevitt, Matthew K. Oliver, Stuart B. Piertney, Paulina A. Szafrańska, Marek Konarzewski & Karol Zub

Conservation Genetics

ISSN 1566-0621
Volume 14
Number 2

Conserv Genet (2013) 14:499-509
DOI 10.1007/s10592-012-0376-4



Springer

Conserv Genet (2013) 14:499–509
DOI 10.1007/s10592-012-0376-4

RESEARCH ARTICLE

Individual variation in dispersal associated with phenotype influences fine-scale genetic structure in weasels

Allan D. McDevitt · Matthew K. Oliver · Stuart B. Piertney · Paulina A. Szafrańska · Marek Konarzewski · Karol Zub

Received: 2 March 2012 / Accepted: 4 June 2012 / Published online: 19 June 2012

Abstract In general, landscape genetic studies have ignored the potential role that the phenotype of individuals plays in determining fine-scale genetic structure in species. This potential over-simplification ignores an important component that dispersal is both condition- and phenotype-dependent. In order to investigate the relationship between potential dispersal, habitat selection and phenotype, we examined the spatial ecology, body mass and fine-scale genetic structure of weasels (*Mustela nivalis*) in Białowieża Forest in Poland. Our study population is characterized by an almost three-fold phenotypic variation in adult body mass and weasels were segregated in certain habitats according to size. We detected significant genetic structuring associated with habitat within the studied area and analyses of radio-tracking and re-capture data showed that the maximum extent of movement was achieved by weasels of medium body size, whereas the smallest and largest individuals exhibited higher site fidelity. With the unrestricted movement of the medium-sized individuals across optimal habitat, genetic admixture does occur. However, the presence of a barrier leads to uni-directional gene flow, with larger individuals outcompeting smaller individuals and therefore maintaining the genetic break in the study area. This highlights the importance of considering both intrinsic (phenotype) and extrinsic (environmental) factors in understanding dispersal patterns and ultimately, gene flow in complex landscapes.

Keywords Anthropogenic barrier · Body mass · Habitat selection · Intra-specific competition · Microsatellites · *Mustela nivalis* · Radio-tracking · Sex-biased dispersal

Introduction

Gene flow (or lack of) between populations is influenced by a multitude of intrinsic (e.g. dispersal ability and breeding system) and extrinsic (e.g. landscape and environmental) factors (Pérez-Espona et al. 2008). It is certainly now well-established that both natural (Pérez-Espona et al. 2008) and man-made (Frantz et al. 2010a) landscape features affect the dispersal ability of animals and this therefore impacts upon gene flow and the genetic structuring of populations (Manel et al. 2003; Storfer et al. 2007). Although one of the goals of landscape genetics is to model and detect successful dispersal in the absence of robust field data (Goldberg and Waits 2010), this can potentially lead to the assumption that the landscape features alone account for limiting dispersal and therefore gene flow between populations. This may represent an over-simplification of how individuals select for and move in/across a landscape.

Electronic supplementary material The online version of this article (doi:10.1007/s10592-012-0376-4) contains supplementary material, which is available to authorized users.

A. D. McDevitt (✉) · M. K. Oliver · P. A. Szafrańska · M. Konarzewski · K. Zub (✉)
Mammal Research Institute, Polish Academy of Sciences, Bialowieza, Poland
e-mail: amcdev@gmail.com

K. Zub
e-mail: karolzub@zbs.bialowieza.pl

A. D. McDevitt
School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland

M. K. Oliver · S. B. Piertney
School of Biological Sciences, University of Aberdeen, Aberdeen, UK

M. Konarzewski
Biology Institute, University of Białystok, Bialystok, Poland

This potential over-simplification ignores an important component that dispersal is both condition- and phenotype-dependent (Clobert et al. 2009). A number of extrinsic factors dictate the decision to disperse, such as the availability of resources (e.g. food/prey, shelter and access to mating opportunities) and fluctuating population densities (Spear et al. 2010). Intrinsic factors also play a role, with variation in physiological, morphological and behavioural traits leading to different patterns of dispersal and habitat preferences among individuals within and between populations (Clobert et al. 2009). Analysis of different species in the same landscape can provide clues to the importance of different traits and specific adaptation to environments in influencing dispersal and gene flow patterns (Goldberg and Waits 2010). However, there still remains a paucity of studies investigating intra-specific differences (e.g. Frantz et al. 2010b).

Body size and condition have emerged as key components of individual dispersal strategies but not always in the same way (Clobert et al. 2009). In some cases, larger individuals have been found to disperse more (O'Riain et al. 1996) but there have been other cases of the dispersing individuals being smaller in size (Hanski et al. 1991). However, these relationships are not always consistent and can change between years, depending on population densities and other factors (Hanski et al. 1991). That this has been relatively ignored in landscape genetics studies has not gone unnoticed (Spear et al. 2010) but it can be difficult to assess these types of relationships within most species.

In order to investigate the relationship between potential dispersal, habitat selection and phenotype, we examined the spatial ecology, body mass and fine-scale genetic structure of weasels (*Mustela nivalis*) in Białowieża Forest in Poland. Our study population is characterized by an almost three-fold phenotypic variation in adult body mass, similar to that found in the rest of the geographic range of this species in Europe (King 1989; Reig 1997; Abramov and Baryshnikov 2000). Body mass is a vital determinant of reproductive success of male weasels, given that they display a polygynous mating system and thus face high intraspecific competition (King 1989). Body mass is also inexorably linked with the rate of energy expenditures (Speakman 2000; Zub et al. 2009), which underpins many other traits, such as fasting endurance and cold-tolerance that will have direct impact on individual survival and lifetime reproductive success. Body mass also drives spatial segregation, which is influenced by the effects of weasels' prey size, which in turn is associated with different habitat occupied by weasels (Zub et al. 2011). Zub et al. (2012a) revealed that body mass was a heritable trait and postulated that spatial differences in body mass results from segregation of individuals of different size, which then select habitats best satisfying their energy needs. We could therefore expect that this may have an effect on fine-scale genetic structure within a heterogeneous landscape. This could lead to patterns of spatial genetic structure that are more complex than those that would be predicted on the basis of habitat alone. Here we investigate the interrelations between habitat, spatial ecology, body mass and genetic structure in weasels in the Bialowieza Forest, Poland.

Materials and methods

Study area, live-trapping and radio-tracking

The study area encompassed the central part of the Białowieża Forest, NE Poland (23°52′E, 52°42′N), including wet sedge marshes in the Narewka river valley, wet meadows and abandoned fields on the Białowieża glade, as well as neighbouring pristine forest protected in the Białowieża National Park. Between 2002 and 2007 weasels were live-trapped within each area (forest, meadows, eastern river valley and western river valley; Fig. 1a) in spring (April–June), summer (July–September), autumn (October–November) and winter (December and January–February). From 20 to 40 traps, spaced about 50 m apart, were placed along transects (1–2 km in length), following fences, ditches and other linear features of landscape, mostly preferred by weasels (Jędrzejewski et al. 1995). Each trapping session lasted for 5–7 days. The number of trapping sessions within each season varied from one to three, according to weather conditions and the density of weasels. When the abundance of animals was low, we restricted trapping effort to one long session in each season, as there were no new weasels during successive trappings events. All weasels were individually marked and results from Capture-Mark-Recapture models indicated that we were able to capture and genotype most individuals from the studied area (Zub et al. 2008, 2011).

Weasels were handled, marked and radio-tracked according to the procedure described by Jędrzejewski et al. (1995). The position of tracked animals was recoded every 15 min during the daylight hours, on several consecutive days. Bearings were taken from a distance of 50–100 m, to avoid disturbance by the observer. Weasels are not active during the night (Jędrzejewski et al. 2000), so only occasionally we checked the position of animals after sunset and before sunrise. From autumn 2002 until winter 2007/2008, we captured and genotyped 164 individuals (40 females and 124 males). Over the same period we radio-tracked 60 animals. These were followed for a relatively short period (on average 14 days, range 2–51 days) during one season, but we repeated observations for the same

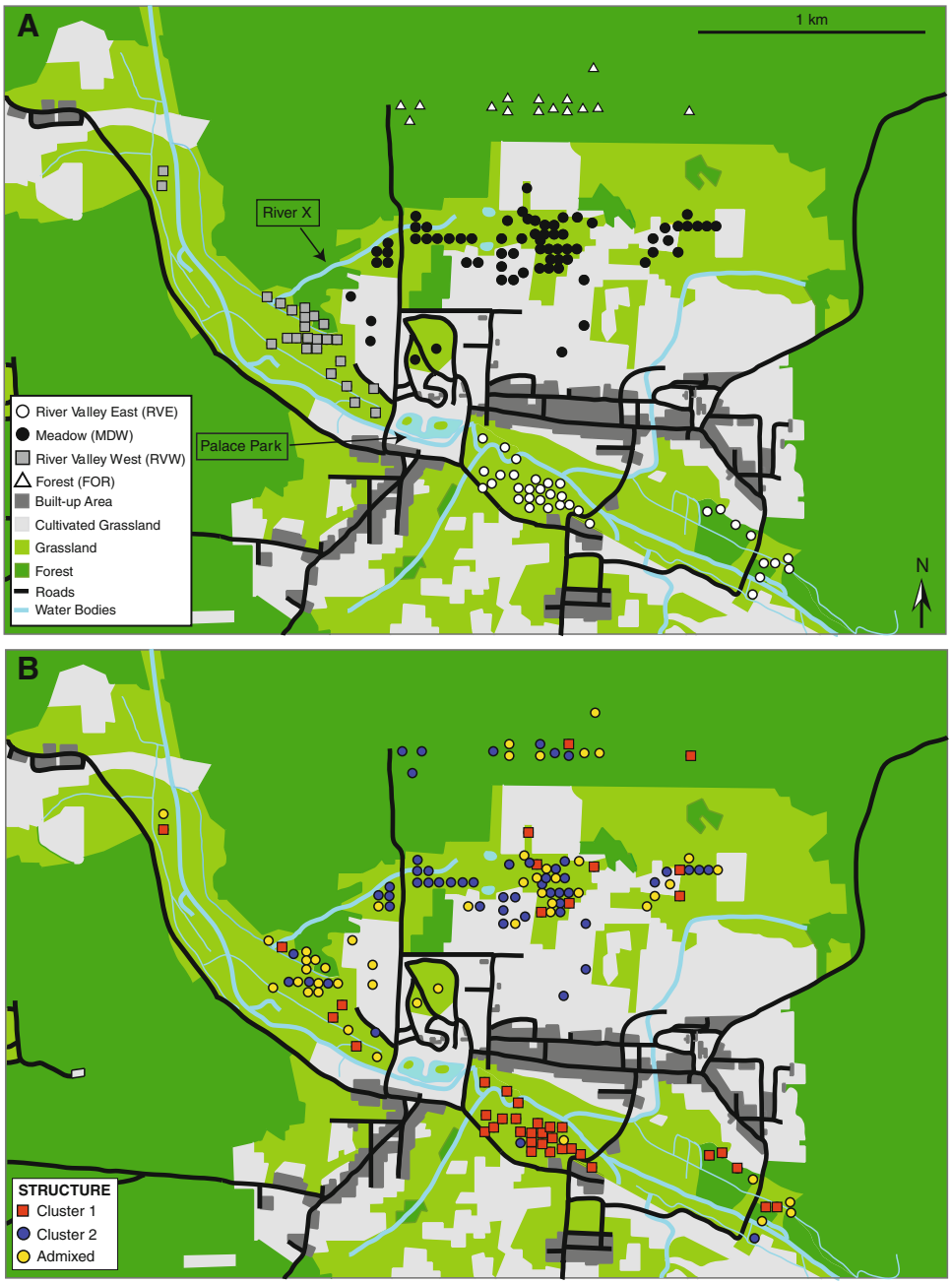


Fig. 1 Capture locations of individuals and population assignments (**a**). Landscape features shown schematically, modified from GIS layers. River X and Palace Park indicated (see "Discussion"). Individuals coloured according to STRUCTURE assignments at $K = 2$ (B). Strongly assigned individuals ($Pr \geq 0.8$) in *red* and *blue* to corresponding clusters, admixed individuals ($0.5 < Pr < 0.8$) in *yellow*. (Color figure online)

individuals in different periods. After each radio-tracking session weasels were captured and radio-collars were removed. The total time of observation for radio-tracked individuals averaged 76 days (2–356 days). Among the radio-tracked weasels there were only two females. For 27 (10 females and 17 males) individuals we collected data only from trapping. For this group the mean time between most distant trapping occasions was 59 days (4–193 days). The remaining 77 weasels were captured only once, or were found dead (seven individuals), mainly in small mammal traps.

Body mass measurements

Weasels are characterised by very high repeatability in body mass measurement (Szafrańska et al. 2007). Each animal was weighed to the nearest 0.1 g prior to metabolic trials in the laboratory (see Szafrańska et al. 2007). This measurement of body mass was usually slightly higher than the body mass determined immediately after capture. In some cases only a single measurement was taken after capture (when found dead for instance), but both measures were highly correlated (Szafrańska et al. 2007).

Genetic analyses

DNA was extracted from tissue samples using the Qiagen Genomic DNA Extraction Kit (Qiagen Ltd.) according to the manufacturer's protocols, and then diluted to approximately 10 ng/μl. All individuals were genotyped at 10 microsatellite loci (Mer0005, Mer0009, Mer0022, Mer0082, Mvi1321, Mvi1381, Mvi1843, Mvis0002, Mvis0022 and Mvis0072; O'Connell et al. 1996; Fleming et al. 1999; Vincent et al. 2003) according to the PCR protocol described in Zub et al. (2012a).

Weasels are typified by high site fidelity in the study area (Zub et al. 2008) so individuals were grouped into four 'populations' within the study area based on capture locations: Forest (FOR); Meadow (MDW) and River Valley East (RVE) and River Valley West (RVW; Table 1; Fig. 1a) for population level analyses. FSTAT 2.9.3 (Goudet 1995) was also used to estimate the inbreeding coefficient, F_{IS}, for each population with significance levels calculated by randomizing alleles among individuals within each population. We then compared this to the observed data to determine deviations from Hardy–Weinberg Equilibrium (HWE), using 10,000 simulations. Tests for linkage disequilibrium between all pairs of loci were carried out. Expected heterozygosity (H_E; Nei 1978) and allelic richness (A_R) for each population was calculated (Table 1).

Pairwise F_{ST} (Weir and Cockerham 1984) was calculated between populations and significance was determined using 10,000 simulations in FSTAT. Pairwise comparisons were corrected for Type I errors using sequential Bonferroni corrections (Rice 1989). Individual-based clustering analysis was first conducted in STRUCTURE v. 2.3.2 (Pritchard et al. 2000; Falush et al. 2003). STRUCTURE was run using the default settings with the admixture model. Ten independent runs were preformed for each K value (1–10) using 500,000 iterations with a burn-in period of 100,000 iterations. The number of clusters (K) was first calculated by obtaining the mean posterior probability of the data [Log probability of data; $Ln\ P(K)$] over the 10 independent runs (Fig. S1). Because of the high number of related individuals in the dataset (Zub et al. 2012a) and the potential for STRUCTURE to overestimate the true K value in these situations (Berry et al. 2004; Bergl and Vigilant 2007), we applied the ΔK method (Evanno et al. 2005), determined by STRUCTURE HARVESTER (Earl and vonHoldt 2012), to estimate the number of clusters based on the rate of change in the log probability of data between successive K values (Fig. S1). We used CLUMPP v. 1.1.1 (Jakobsson and Rosenberg 2007) to determine membership probability to clusters across the 10 runs with a *Greedy* algorithm and 10,000 random permutations. Individuals were considered as belonging to a particular cluster if their assignment probability was high ($Pr \geq 0.8$; Bergl and Vigilant 2007; vonHoldt et al. 2010) and were considered as 'admixed' for inconclusive assignments ($0.5 < Pr < 0.8$). Visualization of individual assignments to clusters per population (see "Results") was performed in DISTRUCT v. 1.1 (Rosenberg 2004).

In our second individual-based analysis, we incorporated the capture location of each weasel, using the spatially-explicit software TESS v. 2.3.1 (Chen et al. 2007). TESS was run using the MCMC algorithm with the admixture model. We first used three initial starting values for the interaction parameter, which represents spatial interactions ($\psi = 0.6$; 0.75 and 0.9) to select the optimal interaction parameter using likelihood ($\psi = 0.6$). Next, ten independent simulations were performed for each K value (2–10) using 50,000 iterations and a burn-in period of 10,000 iterations to identify which K values produced the highest likelihood runs (K_{max}). We then conducted 100 simulations for each K_{max} and estimated membership probabilities were calculated from the 20 highest likelihood simulations for each K_{max} (Chen et al. 2007; McDevitt et al. 2009). Membership assignment to clusters was determined in CLUMPP as described above.

Given the polygynous mating system of weasels, sex-biased dispersal was tested using five different tests (Goudet et al. 2002) available in FSTAT using the predefined populations: F_{IS}, F_{ST}, relatedness, mean Assignment Index and variance of Assignment Indices (see Lampert et al. 2003 for a brief explanation of using each test in relation to sex-biased dispersal).

Table 1 Summary of genetic diversity statistics for each population (see Fig. 1a for population name abbreviations)

Population	N	F_{IS}	A_R	H_E
FOR	17	0.024	7.669	0.777
MDW	78	0.030	7.510	0.769
RVW	28	0.042	8.021	0.812
RVE	41	−0.031	6.801	0.756

N number of individuals per population, F_{IS} inbreeding coefficient, A_R allelic richness corrected for the smallest population size, H_E expected heterozygosity

Body mass, habitat, spatial and genetic structure relationships

Data exploration and linear modelling with residual based model validation (using R) was used to investigate whether variation in weasel body mass could be explained by the habitat type of an individual's location of capture (River Valley, Forest or Meadow), or by its assignment to a genetic cluster as designated by STRUCTURE. Data exploration indicated substantial differences between male

and female body mass, as well as sex-dependent associations between body mass and explanatory variables; as such the two sexes were modelled separately. To allow negative values in accordance with the assumptions of linear regression, body mass was centred by subtracting from the mean, for males and females separately. The explanatory variables STRUCTURE and habitat type were found to be collinear, resulting in substantial changes in parameter estimates if either variable was dropped. As this collinearity was central to the questions being addressed, relationships between the two variables and body mass were modelled separately, and the interactions between the two explored to make biological inferences on the interrelations of body mass, habitat and genetic structure.

We analysed the relationship between body mass and site fidelity in weasels. As dispersal can be difficult to measure directly in short-lived animals such as weasels, we used the maximum extent of movement as a measure of tendency for dispersal (Niitepõld et al. 2009). Weasels are non-territorial and will settle in an area with an adequate food supply, moving on if food becomes scarce (Zub et al. 2008). We collected data on the extent of movement for 86 different weasels (12 females and 74 males). Our estimates were based on radio-tracking combined with trapping (59 individuals) or on trapping only (27 individuals). In both cases we used the maximum linear distance between the two most remote points obtained from radio-tracking or trapping. We also estimated the time elapsed between these two records. For visualization purposes, 100 % Minimum Convex Polygons (MCPs) were calculated to indicate movement and habitat type use during the data collection period.

To estimate the maximum extent of movement in relation to body mass, we used a quantile regression (Koenker 2005), fitting data with linear functions for different τ values. Quantile regression is a natural extension of classical least square regression and is particularly useful for defining limiting effect of covariates by constructing models for upper quantiles of the conditional distribution (Koenker 2005). The significance and standard errors for estimated coefficients were calculated by bootstrapping.

Table 2 Pairwise F_{ST} values between populations (lower diagonal) and corresponding significance value after Bonferroni correction ($P = 0.00833$; upper diagonal)

Population	FOR	MDW	RVW	RVE
FOR		NS	NS	*
MDW	0.0006		NS	*
RVW	0.0037	0.0061		*
RVE	0.0561	0.0600	0.0274	

NS not significant

* Significant

We evaluated the fit of linear models to our data using *F* statistics (ANOVA). We used the extent of movement as a dependent variable and habitat type, gender, time elapsed between records and source of data (radio-tracking or trapping) as predictors. To visualise the relationship between body mass and the extent of movement, we used values of body mass corrected for the effect of habitat type and gender (residuals from linear model). To avoid a possible bias resulted from smaller body mass and less movement of females, and because males are the dispersing sex (see "Results"), we repeated analyses using data collected only for males.

Results

Genetic structure

No evidence of linkage disequilibrium or significant deviation from HWE was found (Table 1). Measures of genetic diversity were highest in the RVW and lowest in the RVE populations (Table 1). Pairwise F_{ST} revealed that RVE was significantly differentiated from all other populations (Table 2). However, no significant differences were observed between the other populations.

Bayesian analysis in STRUCTURE revealed a plateau at $K = 2$ and another at $K = 5$ (Fig. S1). Individual assignment bar plots of both K values in relation to the predesignated populations are shown in Fig. S2. However, the ΔK method (Evanno et al. 2005) revealed a clear peak at $K = 2$ (Fig. S1). Spatially explicit analysis in TESS revealed 3 distinct clusters, largely in agreement with the clusters identified by the ΔK method in STRUCTURE (Fig. S3). Because we are primarily interested in habitat associations that do not necessarily correspond to the spatial proximity of individuals, we shall only focus on the results obtained from STRUCTURE for the remainder of this paper. Individuals strongly assigned ($Pr \geq 0.8$) to Cluster 1 were mainly found in the eastern River Valley (Fig. 1b), with strongly assigned individuals from Cluster 2 mainly located in the Forest/Meadows. The western River Valley was the prime area of admixture, with most individuals being of mixed ancestry (Fig. 1b).

Dispersal was biased towards males in all tests (Table 3) but only tests using F_{ST} and relatedness as measures were significant after Bonferroni correction.

Body mass and spatial ecology

Neither habitat type ($F = 1.14$; $P = 0.33$) or STRUCTURE assignment ($F = 1.14$; $P = 0.33$) explained significant variation in the body mass of female weasels. In contrast, both habitat type and STRUCTURE assignment

Table 3 Tests for sex-biased dispersal with corresponding *P* values

	N	F_{IS}	F_{ST}	Relatedness	Assign. mean	Assign. var.
Females	40	−0.0167	0.0817	0.1533	0.60882	6.99071
Males	124	0.0147	0.0281	0.054	−0.19639	14.65213
P value		0.1798	0.0002*	0.0002*	0.0789	0.0136

NS not significant

* Significance after Bonferroni correction

explained significant variation in the body mass of male weasels (Fig. 2a, b). Males from river valley habitats ($n = 53$) were larger than those from the forest ($n = 9$; $\beta = -21.1$; SE = 6.8; $P = 0.002$) and from meadows ($n = 63$; $\beta = -9.45$; SE = 3.3; $P = 0.005$). Males from meadows were not significantly larger than those from the forest ($\beta = -11.7$; SE = 6.7; $P = 0.085$). Male weasels assigned to Cluster 2 by STRUCTURE ($n = 39$) were significantly smaller than those assigned to both Cluster 1 ($n = 43$; $\beta = 10.6$; SE = 4.0; $P = 0.010$) and the Admixed group ($n = 42$; $\beta = 9.4$; SE = 4.0; $P = 0.019$). There was no significant difference in body mass between males assigned to Cluster 1 and the Admixed group ($P = 0.78$).

Visualization of home ranges (100 % MCPs) and movements between trapping locations can be seen in Fig. 3. The majority of movement occurred between MDW and RVW along the unnamed river indicated (River X; Figs. 1a, 3). The time elapsed between the two records and source of data did not have a significant effect on the extent of home ranges in weasels ($t = 0.24$, $P = 0.80$ and $t = 0.55$, $P = 0.592$, respectively). Simple linear quantile regression for $\tau = 0.95$ demonstrated that the extent of home range significantly decreased along with increasing body mass ($t = -2.24$, $P = 0.03$). The model, which included quadratic and cubic terms of body mass, fitted the data significantly better than the model with linear terms only ($F_{1,78} = 4.23$, $P = 0.02$). This means that the maximum extent of movement was achieved by weasels of a medium body size, whereas the smallest and largest individuals exhibited higher site fidelity (Fig. 4). According to the linear model, the maximum movement extent of males significantly decreased along with increasing body mass ($t = -2.36$, $P = 0.02$), but again the model with quadratic and cubic terms of body mass fitted the data significantly better ($F_{1,67} = 14.49$, $P < 0.001$; Fig. 4).

Discussion

An implicit assumption of landscape genetics studies hitherto is uniformity in how individuals move or disperse across the landscape. However, it has also been recognized that individuals display variation in their likelihood/ability to disperse (Clobert et al. 2009; Spear et al. 2010), which is dependent on both internal state and external factors. For instance, variation in a single gene in the Glanville fritillary butterfly (*Melitaea cinxia*) was linked to flight physiology and therefore dispersal behaviour, demonstrating dispersal variability amongst individuals in the same environment (Niitepõld et al. 2009). In this study, we present evidence from a fine-scale study of weasels demonstrating that phenotypic variation associated with certain environments is an important factor in influencing movement/dispersal patterns and consequently potential gene flow in a heterogenous landscape. While we certainly accept that weasels in our study area are an extreme example of phenotypic variation over such fine spatial scales (males showing three-fold variation in body mass in the study area), our study serves as a caveat for landscape genetic studies assuming that all individuals of a population/species move, select habitat or disperse in the same way.

Analyses of genetic structuring within the area revealed the presence of two distinct genetic clusters (Figs. 1b, S2). F_{ST} analyses revealed that only the eastern part of the river valley showed significant genetic separation from the other populations (Table 2). Bayesian analysis in STRUCTURE clearly pointed to the presence of two clusters (Figs. S1, S2), with most strongly assigned individuals in each cluster broadly found in the eastern river valley RVE (Cluster 1) and in the forest/meadow FOR/MDW (Cluster 2). In general there was a much lower proportion of individuals from Cluster 1 present north of the village of Białowieża (Fig. 1b) than south of it. Areas of human occupation and development are certainly known to act as barriers to dispersal for many species (e.g. Sackett et al. 2012). The village of Białowieża is unsuitable for many reasons, mainly due to high predation risk (domestic cats *Felis domesticus*; stone martens *Martes foina*; and polecats *Mustela putorius* in winter) and a low abundance of suitable prey (Jędrzejewska and Jędrzejewski 1998). The greatest point of admixture was found in the western river valley RVW and the adjacent MDW, suggesting that it is this area in particular where both clusters come into contact (Fig. 1b), resulting in the generally higher levels of diversity being found in RVW (Table 1).

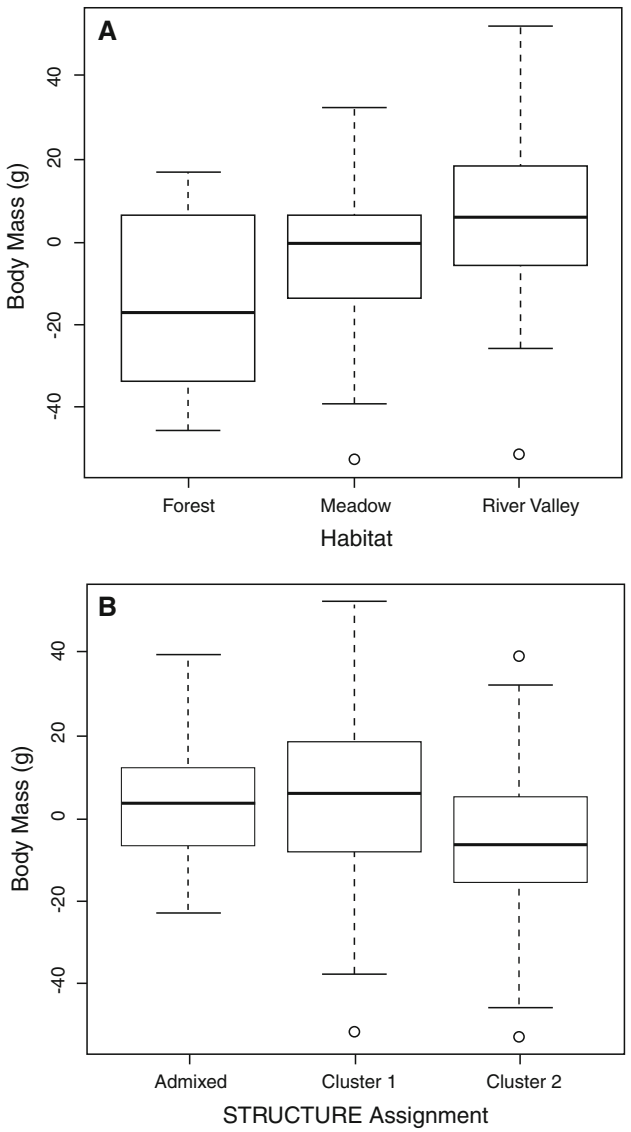


Fig. 2 Body mass of male weasels according to the habitat type in which they were captured (**a**) and the three genetic cluster assignments determined by STRUCTURE (**b**)

We observed no differences in the body mass of females between habitats and given that, as expected, dispersal was sex-biased towards males (Table 3), we shall focus on males for phenotype–habitat associations. Measures of body mass in male weasels indicated a great deal of variability in the study area (Fig. 2a). It was found that weasels occupying the river valley were significantly bigger than those in the meadows, which in turn were bigger than those occupying the surrounding forest (Fig. 2a). In the latter case the difference was only close to statistical significance, though the low statistical power due to relatively few animals having being captured in the forest should be kept in mind. This was confirmed when assigning individuals to the STRUCTURE designations, no difference was found between the Admixed and Cluster 1 (the two assignments found predominantly in the Narewka river valley) but both differed from Cluster 2 (Fig. 2b). Therefore, we can clearly confirm that weasels of varying sizes are distributed non-randomly in this area (Zub et al. 2012a). Although our study was conducted over a limited period of time (2002–2008), Zub et al. (2011) demonstrated that this level of spatial segregation in male weasels of differing body mass has been ongoing over the last 50 years. Therefore, it is clear that this segregation is being maintained and the key to understanding how this happens lies in knowing how these individuals of differing sizes move and select for habitat across the landscape.

It was found that larger individuals and smaller individuals moved less within the study area (Fig. 4), showing higher site fidelity than those of intermediate size. Larger individuals were generally found in the river valley, which is considered optimal habitat for weasels (Zub et al. 2008, 2011) because they offer large and easily accessible prey such as the root vole *Microtus oeconomus*. In the past, the number of weasels in the river valleys of the Białowieża Forest was much lower, because they were outcompeted by the stoat *Mustela erminea* (Sidorovich et al. 1996). The appearance of an invasive predator, the American mink *Mustela vison*, has caused declines in stoat populations, simultaneously releasing weasels from competition with the stoat (Sidorovich and Solovej 2007). This has lead to increased numbers of weasels in the river valleys, as indicated by regularly performed snow tracking (Sidorovich et al. 1996; Zub et al. 2008). In the forest, the main prey species are bank voles *Myodes glareolus* and yellow-necked mice *Apodemus flavicollis* which are small and agile prey (Zub 2004) and perhaps more suitable for smaller weasels. Weasels of intermediate size moved significantly more in the landscape than both small and large individuals (Fig. 4), indicating an increased plasticity in their ability to move to and utilise different habitats.

Radio-tracking and recapture data revealed that most of the movement between habitats occurred in the RVW-MDW area (Fig. 3), with River X acting as a corridor between the habitats (Fig. 1a). During activity periods, weasels select for moist or wet areas (Zub et al. 2008) so this would represent an ideal dispersal path to move between MDW and RVW. This would also certainly explain the large amount of genetic admixture in the area (Fig. 1b). However, there is comparatively little admixture on the east side of the river valley (RVE). This is due to a number of related factors. Two important factors affecting the number of weasels in the river valley are periodic flooding and cyclic changes of prey availability (Zub et al. 2008, 2012a, b). The floods in the Narewka river valley may persist until mid-May and occasionally longer, limiting the space available for both weasels and their prey, or

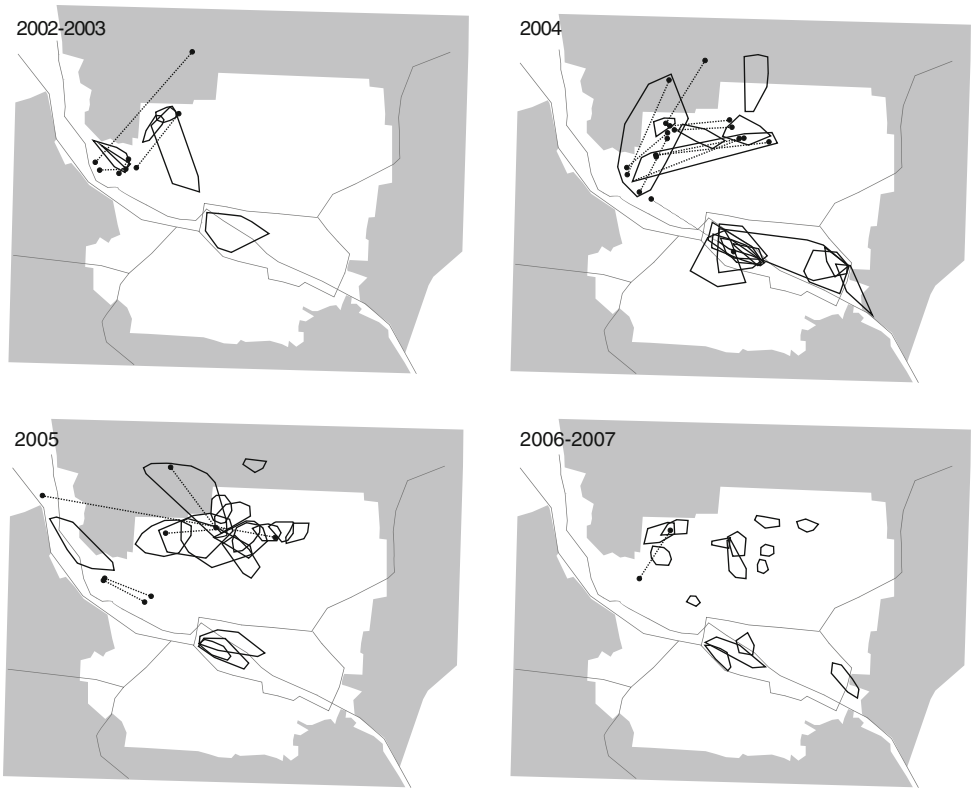


Fig. 3 Radio-tracking and re-capture data separated by year. Maximum extent of movement indicated by 100 % MCPs and re-captures indicated by *dotted lines* between capture points

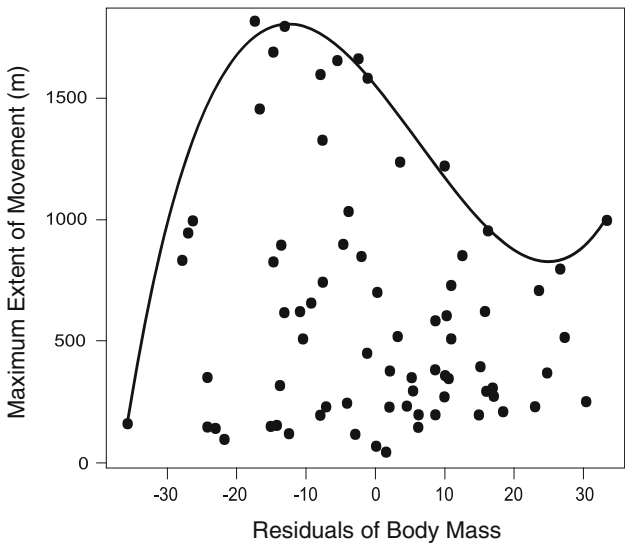


Fig. 4 Relationship between the maximum extent of movement (m) and body mass (corrected for effect of habitat type and gender) for males weasels. The *upper line* (maximum extent of movement) was fitted using quantile regression (for *tau* = 0.95). The data was fitted using the polynomial function of 3rd order

even completely wiping out all animals. The re-colonisation of abandoned areas by small mammals is dependent on the extent of flooding and the availability of suitable habitats in the closest vicinity to the river valley (Wijnhoven et al. 2006). In this respect RVE and RVW differ considerably. The eastern part of the Narewka river valley is squeezed between human settlements or arable land (Fig. 1a), both habitats of which are less suitable for weasels (Brandt and Lambin 2005; Zub et al. 2008) and are lacking in alternative prey. In consequence, weasels are only able to colonise RVE from the east, where huge marshes stretch along the Narewka river into neighbouring Belarus. In contrast to RVE, weasels inhabiting RVW are able to find alternative prey in neighbouring forest and meadows (where the rodent population is driven by different mechanisms; Pucek et al. 1993; Zub et al. 2012b) because there are no barriers to weasel movement/dispersal.

The barrier effect however, plays an important role in maintaining the genetic break between RVE and RVW. The village clearly acts as a barrier (see above) but there is a potential route between the human settlements through the Palace Park (Fig. 1a). This is generally considered unsuitable habitat, but recaptures and genetic data suggests that dispersal does occur across this area (one large male was re-captured in RVW after having being originally caught in RVE in 2004; Fig. 3). Admixture in RVW demonstrates that at least some gene flow occurs but this appears to be unidirectional (Fig. 1b). If prey becomes unavailable for one of a multitude of reasons in RVE, then weasels may be driven west to find alternative food sources. It is generally larger individuals found in RVE so they

would have no problem thriving in RVW. The opposite situation however does not occur. Unrestricted movement occurs between MDW and RVW, which would support the extensive admixture in the west river valley because of the large-scale movement between the habitats, but the Palace Park acts as a filter, with few individuals dispersing through it. Observations of aggressive behaviour between radio-tracked individuals showed that larger males always displaced smaller individuals (Zub 2006). Therefore, the few smaller individuals in RVE would be easily outcompeted for resources and mates (Pertoldi et al. 2006), allowing the observed genetic structure to be maintained between RVE and RVW. This again highlights the importance of individual phenotypic variation in determining fine-scale genetic structure in weasels when a barrier is present.

Weasels clearly differ in their tendency to disperse and settle in certain habitats, depending on both internal and external factors. Body mass is a heritable trait in weasels (Zub et al. 2012a) and individuals select habitats that best suit their energy requirements, outcompeting other, less suited individuals for resources and mating opportunities. When this is coupled with an anthropogenic barrier, it may lead to a more pronounced effect, which may have direct consequences for contemporary evolution and phenotypic change of weasels in this region (Hendry et al. 2008). Body size changes can be dynamic over time and habitat fragmentation can lead to a more rapid response (Schmidt and Jensen 2003). A potential drawback is that this study was conducted over a limited area (Anderson et al. 2010) and it would be interesting to examine the questions addressed here at a larger scale and incorporating more samples, particularly in neighbouring Belarus. It is worth noting that in a large-scale study of weasels in a phylogeographic suture zone, the distribution of mitochondrial lineages were associated with habitat types linked to climate (McDevitt et al. 2012). It would also be beneficial to see if the pattern we report in this study area is replicated elsewhere in its range (Frantz et al. 2010b; Short Bull et al. 2011).

The results of this study clearly have implications beyond understanding fine-scale genetic structure in weasels. It is well established that individuals vary in their dispersal ability (Clobert et al. 2009; Niitepõld et al. 2009) but this is difficult to measure. Here we have demonstrated how phenotype influences dispersal and settlement with direct effects on gene flow. This has important implications for landscape genetic studies, particularly those with the ultimate goal of conserving and establishing better connectivity between populations. We would recommend that a consideration of all the intrinsic and extrinsic factors that can shape the microevolutionary process is required to properly assess the main drivers of genetic structuring in natural populations.

Acknowledgments This study was supported by Ministry of Science and Higher Education grants 3 P04F 05125 to KZ and 2 P04F 01329 to PAS. ADM and MKO were supported by postdoctoral fellowships under the project BIOCONSUS (Research Potential in Conservation and Sustainable Management of Biodiversity), funded by the European Union 7th Framework Programme (FP7 2010–2013; Agreement No. 245737). We would like to thank our numerous students for help in weasel trapping and technical assistance. Finally, thanks to Ilaria Coscia for comments and advice on analyses and to the two anonymous reviewers for their comments on the manuscript.

References

Abramov AV, Baryshnikov GF (2000) Geographic variation and intraspecific taxonomy of weasel *Mustela nivalis* (Carnivora, Mustelidae). Zoosyst Rossica 8:365–402

Anderson CD, Epperson BK, Fortin M-J, Holderegger R, James PMA, Rosenberg MS, Scribner KT, Spear S (2010) Considering spatial and temporal scale in landscape-genetic studies of gene flow. Mol Ecol 19:3565–3575

Bergl RA, Vigilant L (2007) Genetic analysis reveals population structure and recent migration within the highly fragmented range of the Cross River gorilla (*Gorilla gorilla diehli*). Mol Ecol 16:501–516

Berry O, Tocher MD, Sarre SD (2004) Can assignment tests measure dispersal? Mol Ecol 13:551–561

Brandt MJ, Lambin X (2005) Summertime activity patterns of common weasels *Mustela nivalis vulgaris* under differing prey abundances in grassland habitats. Acta Theriol 50:67–79

Chen C, Durand E, Forbes F, François O (2007) Bayesian clustering algorithms ascertaining spatial population structure: a new computer program and comparison study. Mol Ecol Notes 7: 747–756

Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol Lett 12:197–209

Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Res 4: 359–361

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14:2611–2620

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164:1567–1587

Fleming MA, Ostrander EA, Cook JA (1999) Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*). Mol Ecol 8:1351–1362

Frantz AC, Pope LC, Etherington TR, Wilson GJ, Burke T (2010a) Using isolation-by-distance-based approaches to assess the barrier effect of linear landscape elements on badger (*Meles meles*) dispersal. Mol Ecol 19:1663–1674

Frantz AC, Do Linh San E, Pope LC, Burke T (2010b) Using genetic methods to investigate dispersal in two badger (*Meles meles*) populations with different ecological characteristics. Heredity 104:493–501

Goldberg CS, Waits LP (2010) Comparative landscape genetics of two pond-breeding amphibian species in a highly modified agricultural landscape. Mol Ecol 19:3650–3663

Goudet J (1995) FSTAT (version 1.2): a computer program to calculate *F*-statistics. J Heredity 86:485–486

Goudet J, Perrin N, Waser P (2002) Tests for sex-biased dispersal using bi-parentally inherited genetic markers. Mol Ecol 11: 1103–1114

Hanski I, Peltonen A, Kaski (1991) Natal dispersal and social dominance in the common shrew *Sorex araneus*. Oikos 62:48–58

Hendry AP, Farrugia TJ, Kinnison MT (2008) Human influences on rates of phenotypic change in wild animal populations. Mol Ecol 17:20–29

Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23:1801–1806

Jędrzejewska B, Jędrzejewski W (1998) Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Springer, Berlin

Jędrzejewski W, Jędrzejewska B, Szymura L (1995) Weasel population response, home range, and predation on rodents in a deciduous forest in Poland. Ecology 76:179–195

Jędrzejewski W, Jędrzejewski B, Zub K, Nowakowski WK (2000) Activity patterns of radio-tracked weasels *Mustela nivalis* in Białowieża National Park (E Poland). Ann Zool Fennici 37: 161–168

King CM (1989) The natural history of weasels and stoats. Christoper Helm, London

Koenker R (2005) Quantile regression. Cambridge University Press, New York

Lampert KP, Rand S, Mueller UG, Ryan MJ (2003) Fine-scale genetic pattern and evidence for sex-biased dispersal in the túngara frog, *Physalaemus pustulosus*. Mol Ecol 12:3325–3334

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197

McDevitt AD, Mariani S, Hebblewhite M, DeCesare NJ, Morgantini L, Seip D, Weckworth BV, Musiani M (2009) Survival in the Rockies of an endangered hybrid swarm from diverged caribou (*Rangifer tarandus*) lineages. Mol Ecol 18:665–679

McDevitt AD, Zub K, Kawałko A, Oliver MK, Herman JS, Wójcik JM (2012) Climate and refugial origin influence the mitochondrial lineage distribution of weasels (*Mustela nivalis*) in a phylogeographic suture zone. Biol J Linn Soc 106:47–69

Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583–590

Niitepõld K, Smith AD, Osborne JL, Reynolds DR, Carreck NL, Martin AP, Marden JH, Ovaskainen O, Hanski I (2009) Flight metabolic rate and *Pgi* genotype influence butterfly dispersal rate in the field. Ecology 90:2223–2232

O'Connell M, Wright JM, Farid A (1996) Development of PCR primers for nine polymorphic American mink *Mustela vison* microsatellite loci. Mol Ecol 5:311–312

O'Riain MJ, Jarvis JUM, Faulkes CG (1996) A dispersive morph in the naked mole-rat. Science 380:619–621

Pérez-Espona S, Pérez-Barbería FJ, McLeod JE, Jiggins CD, Gordon IJ, Pemberton JM (2008) Landscape features affect gene flow of Scottish Highland red deer (*Cervus elaphus*). Mol Ecol 17:981–996

Pertoldi C, Norup A-M, Madsen AB, Baagoe HJ, Randi E, Loeschcke V (2006) No evidence of past bottlenecks in two Danish mustelids: results of craniometric and genetic studies in time and space. Biol J Linn Soc 88:541–553

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Pucek Z, Jędrzejewski W, Jędrzejewska B, Pucek M (1993) Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. Acta Theriol 38:199–232

Reig S (1997) Biogeographic and evolutionary implications of size variation in North American least weasels (*Mustela nivalis*). Can J Zool 75:2036–2049

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43:223–225

Rosenberg NA (2004) DISTRUCT: a program for the graphical display of population structure. Mol Ecol Notes 4:137–138

Sackett LC, Cross TB, Jones RT, Johnson WC, Ballare K, Ray C, Collinge SK, Martin AP (2012) Connectivity of prairie dog colonies in an altered landscape: inferences from analysis of microsatellite DNA variation. Conserv Gen 13:407–418

Schmidt NM, Jensen PM (2003) Changes in mammalian body length over 175 years—adaptations to a fragmented landscape? Conserv Ecol 7:6

Short Bull RA, Cushman SA, Mace R, Chilton T, Kendall KC, Landguth EL, Schwartz MK, McKelvey K, Allendorf FW, Luikart G (2011) Why replication is important in landscape genetics: American black bear in the Rocky Mountains. Mol Ecol 20:1092–1107

Sidorovich VE, Solovej IA (2007) The stoat *Mustela erminea* population decline in northern Belarus and its consequences for weasels *Mustela nivalis*. N Z J Zool 34:9–23

Sidorovich VE, Jędrzejewska B, Jędrzejewski W (1996) Winter distribution and abundance of predatory mustelids and beavers in the river valleys of Białowieża Primeval Forest. Acta Theriol 41:155–170

Speakman JR (2000) The cost of living: field metabolic rates of small mammals. Adv Ecol Res 30:177–297

Spear SF, Balkenhol N, Fortin M-J, McRae BH, Scribner K (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591

Storfer A, Murphy MA, Evans JS, Goldberg CS, Robinson S, Spear SF, Dezzani R, Delmelle E, Vierling L, Waits LP (2007) Putting the 'landscape' in landscape genetics. Heredity 98:128–142

Szafrańska PA, Zub K, Konarzewski M (2007) Long-term repeatability of body mass and resting metabolic rate in free-living weasels, *Mustela nivalis*. Funct Ecol 21:731–737

Vincent IR, Farid A, Otieno CJ (2003) Variability of thirteen microsatellite markers in American mink (*Mustela vison*). Can J Anim Sci 83:597–599

vonHoldt BM, Stahler DR, Bangs EE, Smith DW, Jimenez MD, Mack CM, Niemeyer CC, Pollinger JP, Wayne RK (2010) A novel assessment of population structure and gene flow in grey wolf populations of the Northern Rocky Mountains of the United States. Mol Ecol 19:4412–4427

Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. Evol 38:1358–1370

Wijnhoven S, Smits AJM, Van der Velde G, Leuven RSEW (2006) Modelling recolonisation of heterogeneous river floodplains by small mammals. Dev Hydrobiol 187:135–152

Zub K (2004) Weasel—hard life of small predator. In: Jędrzejewska B, Wójcik JM (eds) Essays on mammals of Białowieża Forest. MRI PAS, Białowieża, pp 111–120

Zub K (2006) Factors affecting diversity of the body size of weasel (*Mustela nivalis*). PhD thesis, Mammal Research Institute PAS, Białowieża, Poland (in Polish)

Zub K, Sönnichsen L, Szafrańska PA (2008) Habitat requirements of weasels *Mustela nivalis* constrain their impact on prey

populations in complex ecosystems of the temperate zone. Oecologia 157:571–582

Zub K, Szafrańska PA, Konarzewski M, Redman P, Speakman JR (2009) Trade-offs between activity and thermoregulation in a small carnivore, the least weasel *Mustela nivalis*. Proc R Soc Lond Ser B 276:1921–1927

Zub K, Szafrańska PA, Konarzewski M, Speakman JR (2011) Effect of energetic constraints on distribution and winter survival of weasel males. J Anim Ecol 80:259–269

Zub K, Piertney S, Szafrańska PA, Konarzewski M (2012a) Environmental and genetic influences on body mass and resting metabolic rates (RMR) in a natural population of weasel *Mustela nivalis*. Mol Ecol 21:1283–1293

Zub K, Jędrzejewska B, Jędrzejewski W, Bartoń K (2012b) Cyclic voles and shrews and non-cyclic mice in a marginal grassland within European temperate forest. Acta Theriol. doi:10.1007/s13364-012-0072-2